

EFFECTS OF PREY QUALITY ON THE LIFE HISTORY OF A HARVESTMAN

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ABSTRACT. Information on the value of various food types for harvestmen is sparse. The aim of this study was, therefore, to clarify the quality of six different food types to a harvestman. Survival, growth and development were used as measures of fitness in a laboratory experiment. Recently hatched *Oligolophus tridens* were fed the following experimental diets until maturity: *Drosophila melanogaster* (Diptera), entomobryid Collembola (*Tomocerus bidentatus*/*Sinella curviseta*), *Folsomia candida* (Collembola), *Sitobion avenae* (Aphidoidea), *Rhopalosiphum padi* (Aphidoidea), and a mixed diet containing the five prey types. Survival and growth rate were high on the *D. melanogaster* and entomobryid diets, and low on the *F. candida*, *S. avenae* and *R. padi* diets. The mixed diet caused a high early mortality, later a good survival and a high growth rate. The majority of harvestmen on the *D. melanogaster* and entomobryid diets matured. None of the harvestmen fed pure aphid diets developed beyond the fourth instar, and only few from the *F. candida* diet matured. Overall, the diets separate in three levels: *D. melanogaster* and the entomobryid diet were high-quality, the mixed diet was intermediate, and the two aphid diets and *F. candida* diet were low-quality. In general, the quality ranking agrees with that of other generalist predators, though there are differences in details.

Keywords: Opiliones, *Oligolophus tridens*, fitness, diet

Harvestmen are omnivorous generalists, with a variety of feeding habits, ranging from plant eating to predation. They eat a range of small invertebrates, which are probably caught live and killed. Examples of the invertebrate diet are: springtails, aphids, snails, earthworms, other harvestmen and spiders (Sankey & Savory 1974). Harvestmen are also scavengers and will scavenge both on invertebrates (Sankey & Savory 1974) and vertebrates (Sankey 1949). Studies have shown that harvestmen generally prefer small prey, such as Hemiptera and Collembola (Adams 1984). In the laboratory, harvestmen have successfully been fed odd diets, e.g., bananas, cooked vegetables, ham, cream cheese (Gnaspi 1996), dried eggs, whole meal flour, yeast (Todd 1949), together with live animal food. Gnaspi (1996) tested which food types the harvestman *Goniosoma spelaeum* (Mello-Leitão 1932) will accept and came to the conclusion that these harvestmen should be considered “omnivores tending to carnivory”. There are only few laboratory studies of the feeding ecology of harvestmen, so information on the quality of specific diets is very sparse.

Laboratory studies on the quality of differ-

ent food types have been conducted on several generalist predators such as spiders (Toft 1995; Toft & Wise 1999a) and carabid beetles (Bilde & Toft 1999). The quality of different prey can be evaluated by comparing fitness parameters of the predator kept on different dietary treatments. Different fitness parameters can be used as quality measures: survival, body mass, time used in development, size of body parts, fecundity etc. In this study, survivorship, growth and development were used. Young harvestmen (*Oligolophus tridens* (C.L. Koch 1836)) were reared on six diets and the quality of each diet was assessed by comparison of the fitness measures. In the experiment we tested monotypic diets of a fly, two springtails, two aphids, and a mixed diet of all five. These prey types were chosen because they represent ordinary harvestman prey from different invertebrate orders and most of the prey can be found in the same habitats as *O. tridens*. Furthermore, the aphids (*Sitobion avenae* (Fabricius) and *Rhopalosiphum padi* (Linnaeus)) are pests in agricultural fields, and are among the most abundant aphids in cereal fields (Wikteli 1982).

The prey types used in the present study

have been evaluated in other studies of generalist predators as well. In the light of these results we expected that fruit flies, *Drosophila melanogaster* (Meigen), and the entomobryid springtails *Tomocerus bidentatus* (Folsom)/*Sinella curviseta* (Brook) would be of good quality to the harvestmen (Toft & Wise 1999a; Vanacker et al. 2004). The aphids *S. avenae* and *R. padi* and the collembolan *Folsomia candida* (Willem) are of poor quality to spiders and carabid beetles. Only a few individuals molted when wolf spiders (*Pardosa prativaga* (L. Koch 1870)) were fed the aphids (Toft 2000). Wolf spiders (*Schizocosa* sp.) fed *F. candida* survived for a shorter period than the starved controls (Toft & Wise 1999a) and *F. candida* was therefore considered a toxic prey. We expected that these findings would also apply to harvestmen, because both wolf spiders and harvestmen are generalist predators and can be found in the same habitats. It is more difficult to predict the consequences of the mixed diet. The effect depends on the effect of each prey type, how much the harvestmen eat of each prey and if there is an interaction of the effects between some of the prey when harvestmen are fed a mixed diet.

METHODS

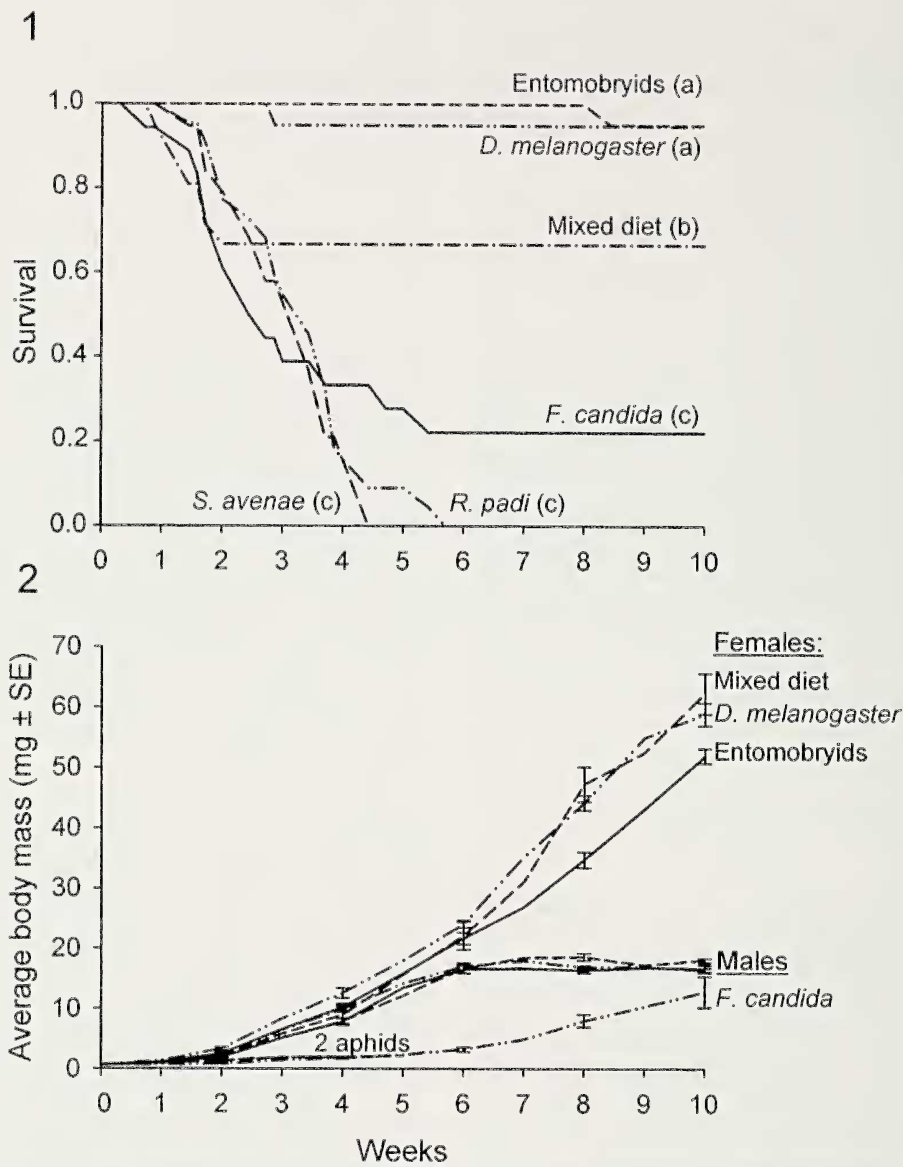
The harvestman.—The harvestman *Oligolophus tridens* occurs all over northern and central Europe (Martens 1978) and has also been reported from North America (Bell 1974). The species is abundant in Denmark and can be found in a variety of habitats, especially in woodlands, roadsides and in gardens. The harvestman has a body length of 4–5 mm (males) or 5–6.5 mm (females) (Sankey & Savory 1974). The life cycle is annual and the harvestmen overwinter in the egg stage. Hatchlings emerge in spring (in Denmark April–May, Meinertz 1964; per. obs.). The first molt takes place a few hours after the harvestmen emerge from the egg (Martens 1978) and they pass through 6 juvenile instars before they mature (Pfeifer 1956; Phillipson 1962).

Prey.—All the prey animals came from laboratory cultures. The prey was freeze killed and provided in surplus amounts. Wild type fruit flies (*Drosophila melanogaster*) were reared on instant *Drosophila* medium (Formula 4–24, Carolina Biological Supply; Burlington, NC, USA) mixed with crushed dog

food (Techni-Cal® ADULT, Martin Pet Foods, Ontario, Canada) in a proportion of 100 g of *Drosophila* medium to 54.5 g dog food. The enrichment ensured a high nutritional quality of the flies, especially regarding proteins. Enriched fruit flies increased growth and survival in a wolf spider (Mayntz & Toft 2001) and supported a high egg production in a carabid beetle (Bilde et al. 2000). *Folsomia candida* was raised on baker's yeast. The entomobryids *Tomocerus bidentatus*/*Sinella curviseta* were both raised on baker's yeast and *Drosophila* medium. At the beginning of the experiment the harvestmen in the entomobryid group were fed *T. bidentatus*, but as the culture was slow and there was a risk of food shortage, the harvestmen were fed *S. curviseta* from week 6. Both *T. bidentatus* and *S. curviseta* are considered to be prey of high quality (*T. bidentatus*: Toft & Wise 1999a; *S. curviseta*: Vanacker et al. 2004). *Rhopalosiphum padi* and *Sitobion avenae* were both raised on wheat seedlings of mixed cultivars. Mixed stages of springtails and aphids were used to feed the harvestmen.

The experiment.—Young *O. tridens* in the second instar were collected in a small forest near Århus, Denmark, 56°07'N, 10°00'E, in late April 2003 by sifting leaf litter over a white tray. The harvestmen were kept individually in plastic tubes (diameter 2 cm, height 6 cm) with a moistened bottom layer of plaster mixed with charcoal and a foam rubber plug. Throughout the experiment the harvestmen were kept at a constant temperature of 17 °C, and a photoperiod of 16L:8D. The harvestmen were weighed the day after collection and assigned to one of six diet treatments with roughly the same distribution of body masses. The treatments were: *D. melanogaster*, *T. bidentatus*/*S. curviseta* (both Entomobryidae), *F. candida* (Isotomidae), *S. avenae*, *R. padi*, and a mixed diet with about equal amounts of the five prey types. Some of the replicates were discarded because of escapes and accidents. The number of replicates in each treatment therefore varied from 18–22. The harvestmen were transferred to larger plastic tubes (diameter 3.5 cm, height 8 cm) after the third molt.

Prey and water were renewed, and mortality and molts were checked three times per week. The duration of instar 2 was recorded as the number of days from collection to the next



Figures 1-2.—1. Survivorship curves for harvestmen *Oligolophus tridens*. The harvestmen were raised in the laboratory from the second instar to maturity on six different diets. Curves with different letters are significantly different. 2. Growth curves for harvestmen *Oligolophus tridens*. The harvestmen were raised in the laboratory from the second instar to maturity on six different diets. “Males” are males from the diets: *Drosophila melanogaster*, entomobryid springtails and mixed diet. Harvestmen fed aphids died before the sex could be determined. *Folsomia candida* data for males and females were pooled because of the low number. Error bars are only shown every second week for the sake of clarity.

molt. A few molts were missed. As the molts progressed synchronously within each diet treatment a molt date was estimated for the missing molts, using the average molt date for the harvestmen in the same treatment. When a molt was observed, the midpoint between two days in which the tubes were checked,

was used to compute the parameter “days in instar”. The harvestmen were weighed weekly (Sartorius electronic balance MC5; 0.001 mg accuracy) to measure growth rate. The most recent weighing before the molt was used for the parameter “weight at molt”. The experiment was terminated after 10 weeks.

Statistical analysis.—The survivorship data were tested with the Log Rank test (Pyke & Thompson 1986). The pairwise Log Rank comparisons were not corrected with sequential Bonferroni adjustment (Moran 2003), because the prey types were chosen based on prior assumptions and the relatively high number of prey types would make it unreasonably difficult to obtain any significance after adjustment. The growth curves were compared using multivariate analysis of variance (MANOVA) with repeated measures, with time (weeks) as the repeated factor. The time * diet interaction term was used to detect differences in growth over time between the treatments. However, animals that died before the end of the experiment were excluded from the analysis. We analyzed the growth data for all treatments for only three weeks or approximately 50% of their maturation time, at which time there were still harvestmen in all treatments. Body mass changes from start of the experiment to week three were tested with one-way ANOVA. The data were log transformed to achieve variance homogeneity (Levene's test $\alpha > 0.05$). A post hoc test was used to locate the differences indicated in the overall ANOVA; because the treatments were chosen to test potential harvestman food, and all the comparisons therefore were planned, a Student's t-test was applied. For the treatments: *D. melanogaster*, entomobryids and the mixed diet, repeated measures analysis of body mass was carried out for the full experimental period. The duration of the instars and the "weight at molt" were analyzed with one-way ANOVA. The data were transformed when the assumption of homogeneity of variance was not met (for details, see Results). Post hoc mean comparisons between treatments were done with Student's t-test. Furthermore a two-way ANOVA was used to test for any interaction between sex and treatment on development. All statistical analyses were performed with JMP 5.0 for windows (SAS institute).

RESULTS

Survivorship.—There was an overall significant treatment effect on survival (Log Rank test, $\chi^2_5 = 78.7382$, $P < 0.0001$, Fig. 1). The pairwise comparisons separated treatments into three groups: *D. melanogaster* and the entomobryids were of the same high qual-

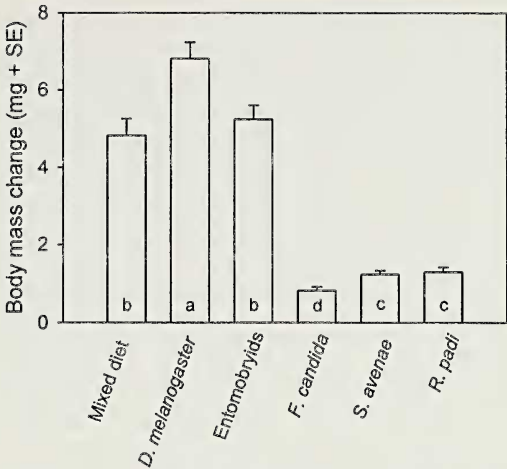


Figure 3.—Body mass change in the harvestman *Oligolophus tridens*, from the beginning of the experiment to week 3 (mg, mean + SE). Bars with different letters are significantly different (ANOVA, Student's t-test).

ity. The mixed diet was intermediate and the two aphids and *F. candida* were of low quality. Four individuals from the *F. candida* diet survived to the end of the experiment. None of the aphid-fed harvestmen survived.

Growth.—For the first three weeks there was a significant overall time * diet interaction on the body masses (MANOVA, $n = 86$, Wilk's $\lambda = 0.1355$, $F = 15.2856$, NumDF = 15, DenDF = 215.73, $P < 0.0001$, Fig. 2). The ranking of the diets was: *D. melanogaster* > entomobryid = the mixed diet >> the two aphid diets > *F. candida*. This is supported by an ANOVA test on the body mass change over the first three weeks of the experiment (overall ANOVA test on ln-transformed data, $n = 86$, $F_{5,80} = 94.9672$, $P < 0.0001$, Fig. 3). The repeated measures test was also done for the first three weeks on the animals that matured (from the treatments *D. melanogaster*, entomobryids and mixed diet), with both treatment and sex as factors. The test showed that there was no significant time * diet * sex interaction on the body mass (MANOVA, $n = 53$, Wilk's $\lambda = 0.9305$, $F = 0.5502$, NumDF = 6, DenDF = 90, $P < 0.77$). There was a significant time * diet interaction on the body mass among the females from the high-quality treatments over all 10 weeks of the experiment (MANOVA, $n = 26$, Wilk's $\lambda = 0.0528$, $F = 4.6934$, NumDF = 20, DenDF = 28, $P < 0.0001$). Contrast tests showed that

the three diets all differed in body mass over time ($P < 0.006$), though *D. melanogaster* and mixed diet ended up at the same level. If males were included in the test there was a significant time * diet * sex interaction on the body mass over 10 weeks (MANOVA, $n = 53$, Wilk's $\lambda = 0.2133$, $F = 4.4273$, NumDF = 20, DenDF = 76, $P < 0.0001$).

Development.—The harvestmen were in the second instar at collection. The maturation success was high on the *D. melanogaster* (95%), and the entomobryid (100%) diets, and the majority of harvestmen from the mixed diet matured (67%). Development was restricted on the aphid and *F. candida* diets and many of the harvestmen on these diets never molted. None of the harvestmen fed aphids molted to the fifth instar and only 19% from the *F. candida* diet matured. Generally the harvestmen from the *D. melanogaster* and mixed diet were the fastest to complete an instar and harvestmen from the *F. candida* treatment were the slowest (Fig. 4, right column). The total number of days from collection to the last molt showed a significant effect of diet (ANOVA test on ln-transformed data, $n = 58$, $F_{3,54} = 58.2450$, $P < 0.0001$). The harvestmen from the *D. melanogaster* diet were the first to complete their development (39.0 ± 0.68 days, mean \pm SE), mixed diet and the entomobryid took a few days more (41.1 ± 0.62 ; 43.6 ± 0.86) and those from *F. candida* were the last (68.5 ± 3.06 days). As to the "weight at molt", the *D. melanogaster* and entomobryid diets resulted in the heaviest animals and the *F. candida* diet resulted in a low body mass, which is particularly evident at the last molts (Fig. 4, left column). Both male and female data are included in Fig. 4. After five weeks the sex of the surviving harvestmen became apparent. The males reached a body mass of approximately 17 mg which was maintained with minor fluctuations (Fig. 2). The females increased their body mass considerably after maturation. A two-way analysis of variance was used to test for any sex-specific growth patterns (only the animals that matured from the treatments: *D. melanogaster*, entomobryids and mixed diet). There was no interactions (treatment * sex, $P > 0.11$), but there were significant effects of sex on the duration of instar 2, 5 and 6; and on the weight at the 6th molt (Table 1).

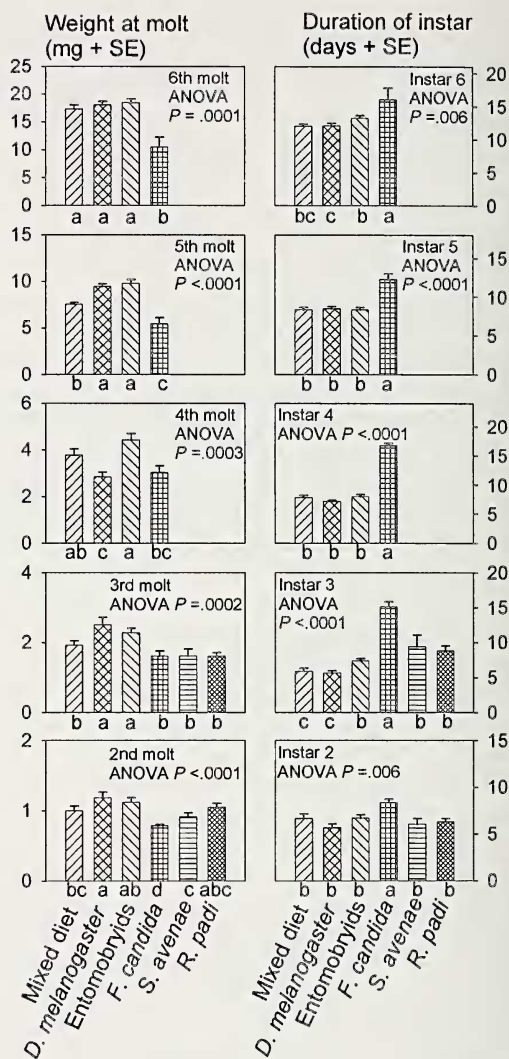


Figure 4.—Weight at molt (mg, mean + SE) and duration of instars (days, mean + SE) of harvestmen, *Oligolophus tridens*, reared on six diets. The dataset were tested with ANOVA, data were transformed if necessary. Overall P -values indicate significance. Pair wise comparisons were made with Students t -test; bars with different letters are significantly different. Male and female data are pooled in the figures.

DISCUSSION

When the three fitness parameters, survival, growth and development are combined, the overall conclusion is that the diets separate in three different quality levels. The two aphids, *S. avenae* and *R. padi*, and the springtail *F. candida* were low-quality diets; both diets affected survival and growth. The development of the harvestmen was slow on the *F. candida*

diet, whereas harvestmen on the two aphid diets were only slightly slower than from the high-quality diets. Overall the mixed diet was of intermediate quality. It was of high quality regarding growth and development. Among the small juvenile harvestmen, the mixed diet caused a high mortality, an affect not seen in older animals. *Drosophila melanogaster* and entomobryids were high-quality prey, with respect to all three parameters. These results agree in general with the findings of other studies of generalist predators. *Drosophila melanogaster* and entomobryids have been reported to be of high quality to spiders (Toft & Wise 1999a; Mayntz & Toft 2001). Aphids are usually found to be of low quality to spiders (Toft 1995, 2000) and beetles (Bilde & Toft 1999), and *F. candida* was classified as a toxic prey to wolf spiders (Toft & Wise 1999a). A pronounced sexual size dimorphism was detected in the present experiment. The growth of the males stopped when the males were subadult, whereas the females gained body mass throughout the experiment and became much larger than the males. A large body mass is more important for females than for males, because females invest more in reproduction. The result of this fecundity selection is that females often are larger than males in invertebrates (Head 1995). The females in this experiment were generally faster to complete an instar and they reached maturity about 3 days before the males.

In a study on linyphiid spiders, Toft (1995) found that when the females were fed normal fruit flies, the hatching success of the spider eggs was high for the first two or three egg sacs, but then the hatching success declined. The quality of fruit flies can be improved by enrichment of the media with extra proteins, for example by adding dog food (Mayntz & Toft 2001). However, even a fruit fly diet, with or without enrichment, has its restrictions. Although it was the best prey of the study, protein enriched fruit flies was not fully sufficient for a wolf spider, as mortality and molting failures were higher than expected (Mayntz & Toft 2001). In the present study, mortality was low on the fruit fly diet and there were apparently no molting failures.

The effects of mixed diets are varied. Some studies have shown that dietary mixing is beneficial and essential to survival and development (Lowrie 1987; Uetz et al. 1992), others

that it depends on what the mixed diet consists of, i.e. it has to be the right mix (Marcussen et al. 1999; Toft & Wise 1999a). In this study the mixed diet caused a high mortality at the beginning, which might be due to the low-quality parts of the diet, i.e., *F. candida* and the aphids. If low-quality and potentially toxic prey comprise a large part of the diet, a mixed diet may not be beneficial. Those that survived the first few weeks may either have had a physiological tolerance to the low-quality prey or been able to reject them. If the surviving harvestmen in the mixed diet group developed an increased preference for the high-quality prey, their diet basically consisted of a mix of two high-quality preys. If high-quality prey is provided, there might be no or even negative effects of adding other prey types. In this study it seems that a monotonous high-quality diet, as for example *D. melanogaster* or the entomobryids, is better than a mixed diet of high-quality and low-quality or potentially toxic elements.

In this experiment the *F. candida* diet was of low quality to the harvestmen, both regarding survival, growth and development. Some of the harvestmen from the *F. candida* treatment survived, gained weight and molted to maturity. This shows that they did eat *F. candida* and that some of the harvestmen must have been more tolerant to the potentially toxic components in this diet than others. *Folsomia candida* is toxic to spiders, as spiders fed *F. candida* died faster than starved controls (Toft & Wise 1999a) and they cannot complete their development on a diet of pure *F. candida* (Fisker & Toft 2004); furthermore *F. candida* induced a specific feeding aversion in a spider (Toft & Wise 1999b). It was therefore a surprise that some of the harvestmen in the present experiment survived and developed. This could indicate genetic variation in the ability to cope with the toxic collembolan (cf. Beck & Toft 2000). It is possible that at least some of the harvestmen are better able to overcome the chemical defenses in *F. candida* than the spiders are. The harvestman *Mitopus morio* (Fabricius 1799) can tolerate the defensive alkaloids of their leaf beetle prey, by avoiding bioactivation and by rapid elimination of the detoxification products via the feces (Hartmann et al. 2003). Perhaps a similar process is operating in *O. tridens*, but with a high variation in individual ability to tolerate

Table 1.—Weight at molt (mg, mean \pm SE) and duration of instar (days, mean \pm SE) in male and female *Oligolophus tridens* from the treatments: *Drosophila melanogaster*, entomobryids and mixed diet. Only animals that matured are included in the tests. Welch ANOVA was used if the assumption of homogeneity of variance was not met. Asterisks indicate level of significance (* P < 0.05, ** P < 0.01, *** P < 0.001).

	Weight at molt (mg)			Duration of instar (days)		
	♂	♀		♂	♀	
2nd molt/instar 2	1.09 \pm 0.06	1.16 \pm 0.07	—	7.15 \pm 0.33	5.74 \pm 0.34	**
3rd molt/instar 3	2.24 \pm 0.15	2.26 \pm 0.15	—	6.40 \pm 0.30	6.23 \pm 0.31	—
4th molt/instar 4	3.72 \pm 0.22	3.67 \pm 0.23	—	7.59 \pm 0.25	7.71 \pm 0.26	—
5th molt/instar 5	9.13 \pm 0.28	8.80 \pm 0.29	—	8.68 \pm 0.22	7.99 \pm 0.22	*
6th molt/instar 6	16.65 \pm 0.50	19.42 \pm 0.53	***	12.92 \pm 0.31	11.86 \pm 0.32	*

F. candida. It is possible that freeze-killing of the prey, as used in this study, can alter the chemical composition, compared to live animal prey. However, a study of the carabid beetle *Bembidion lampros* (Herbst) showed that freeze-killing did not change the palatability of the springtails used as food (Bilde et al. 2000).

The few harvestmen fed *F. candida* that survived and matured obtained a lower body mass compared to the harvestmen from the other three diets. It is possible that *F. candida* contains toxic substances that impede development. In a study of a linyphiid spider it was suggested that *Folsomia fimetaria* (Linnaeus) "contains an element that inhibits digestion" (Marcussen et al. 1999). A similar result was seen in a study of a wolf spider (*Pardosa prativaga*) in which *F. candida* apparently inhibited the utilization of a better quality prey (*D. melanogaster*) (Fisker & Toft 2004). *Pardosa prativaga* compensated for the toxic effect of *F. candida* by increasing the intake of *D. melanogaster*, but the spiders still showed a higher mortality and grew more slowly than spiders fed only *D. melanogaster* (Fisker & Toft 2004). If the harvestmen on the mixed diet ate *F. candida*, they might have been exposed to toxins that decrease the digestion and/or utilization of the high-quality parts of the diet, and thereby caused a high mortality in the first few weeks. The high early mortality in the mixed diet and in the *F. candida* diet can also be explained by the size of the harvestmen. Studies have shown that small juvenile wolf spiders are more dramatically affected by *F. candida* than are larger juveniles

(Toft & Wise 1999b; Fisker & Toft 2004). This also seems to be the case for harvestmen.

Low ranking of aphids as food is widespread among generalist predators (Bilde & Toft 1994, 1999; Toft 1995). This experiment shows that *O. tridens* cannot survive on a pure aphid diet. High mortality was also the result in an experiment with larvae of the staphylinid beetle *Tachyporus hypnorum* (Fabricius) (Kyneb & Toft 2004). Aphids can also affect development. Wolf spiders (*Pardosa amentata* (Clerck 1757)) were unable to go through the first molt, and all the spiders died within two weeks, when fed a pure aphid diet (Toft 1995). These studies also indicate a limitation on the quantity of aphids the spiders and beetles can tolerate (Bilde & Toft 1994; Toft 1995). The food consumption was not measured in the present experiment, but it is very likely that the harvestmen consumed considerably fewer aphids than fruit flies. The prey in this study was freeze killed, before being offered to the harvestmen. This process neutralized the siphuncular defense system of the aphids, making predation easier (Toft 1995). The low quality of the aphid diet must therefore rely on a deterrent or toxic substance in the aphids which prevents the harvestmen from utilizing the nutrients. Dixon & McKinlay (1989) studied aphid predation by harvestmen in a potato field. They state that opilionids have been neglected and probably undervalued as predators of crop pests. A microcosm study with *R. padi* and different generalist predators showed that *O. tridens* was the most efficient predator; reducing aphid numbers up to 97% as compared to predator-free controls (Madsen et al. 2004).

These studies of aphids and harvestmen are in contrast to our results, from which it seems unlikely that harvestmen, at least not *O. tri-dens*, can act as a powerful biocontrol agent. Harvestmen may, however, contribute to the combined effect of the generalist predator complex on aphid population growth (Symondson et al. 2002).

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